FLUCTUATIONS IN ABUNDANCE OF BURROWING MAYFLIES IN SOUTHERN INDIAN LAKE, MANITOBA: MECHANISMS AND IMPLICATIONS FOR ENVIRONMENTAL MONITORING

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Graduate Studies

The University of Manitoba

by

Donna J. Giberson

in Partial Fulfilment of the

Requirments of the Degree

of

Doctor of Philosophy

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BY

DONNA J. GIBERSON

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

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ERRATUM

Note that the page numbers 29, 84, and 161 are missing, although the text is intact. Those page numbers were inadvertently left out during typing.

ABSTRACT

In the mid-1970's, Manitoba Hydro impounded Southern Indian Lake (SIL) and diverted much of the flow of the Churchill River into the Nelson river catchment for hydroelectric power generation. A subsequent dramatic decline in burrowing mayfly (*Hexagenia*) populations was originally attributed to the manipulation, until recovery of the population was observed despite ongoing physical impacts from impoundment and diversion. In 1986, an intensive study on *Hexagenia* in SIL was implemented to determine the actual mechanisms controlling population abundance in the lake to aid in the interpretation of the long-term monitoring data.

The major factors affecting the population dynamics of *Hexagenia* in SIL during the study period were related to weather variables, primarily water temperature during development (and its relationship to air temperature during the open water period) and weather conditions (wind, air temperature) during the emergence period. The two species in the lake, *H. limbata* and *H. rigida*, approach their northern range limit at or near SIL. Their life cycles were similar in the study regions and closely related to thermal regime; requiring 3-yr in warmer areas of SIL and 4-yr in the coldest study region. Subimago emergence occurred from mid-July to mid-August in warm years and warm locations, but not until September in colder years or regions. September weather at SIL was often stormy and cold, and these conditions hindered emergence success. After emergence, transformation to the adult (imago) stage was dependent on air temperatures; the final moult required ≈24-48 h at 10-25°C and was unsuccessful at very low temperatures (near 0°C).

Size of nymphs at maturity was related to thermal regime and the length of the life cycle. Mean body length of mature nymphs declined with decreasing thermal regime in the lake regions where 3-yr life cycles predominated. In

the coldest region investigated, where the life cycle length increased from 3-yr to 4-yr, body size was similar to that from the warmest location. Body size in the female was strongly correlated to fecundity (number of eggs/female); therefore, mean fecundity showed the same relationship to temperature as body size.

The link between nymphal development and temperature was confirmed in laboratory studies. Growth was noted at all temperatures evaluated (8°, 10°, 12.5°, 15°, and 20°C), and growth rates increased with increasing temperature for both species. Variations in growth rate affected both the time required for development and the size at maturity. Total development times (from egg hatch to first emergence) were 380 d at 15°C compared to only 183 d at 20°C, and individuals reared at 15°C were smaller and less fecund than those reared at 20°C. Growth and development was also affected by food availability: nymphs reared under limiting food conditions took longer to develop and adults were smaller and less fecund than those reared under non-limiting food conditions. Nymphal rearing density, at levels ranging from 215 to 1290 nymphs/m^2, had no significant effect on growth.

Egg hatch was related to temperature. Eggs hatched at temperatures from 8°C to 20°C (the highest temperature evaluated), but not at 4°C. Fewer eggs hatched and the time required for hatch was extended at the lower temperatures. Egg hatching success was improved by subjecting eggs to cold temperatures (4°C) during development. In addition, experiments indicated a bimodal hatching response in the eggs: some eggs hatched immediately if conditions were favourable, and the remainder apparently required exposure to cold to initiate hatch.

Abundance and distribution of nymphs in the lake was related to thermal regime. The greatest abundance was noted in the warmest locations, and

numbers declined with decreasing temperature. Temperature affected abundance through its effects on life history parameters: lower relative temperatures resulted in longer life cycles and higher accumulated mortality, fewer eggs hatching, and delayed emergence with a higher probability of temperature- or storm-related impacts on emergence and mating.

Between-year weather differences should result in similar weather-related fluctuations in abundance as were noted between regions, and two consecutive very cold years (1978 and 1979) coincided with the inception of hydroelectric development. Over the 15-yr monitoring period, ≈95% of the variation in whole-lake abundance of burrowing mayflies (R^2=.947) could be explained by air temperature. Therefore, the overall decline in *Hexagenia* numbers, originally thought to be anthropogenic, was more likely a response to weather.

Regionally, however, the *Hexagenia* response to air temperature was not uniform throughout the lake. In part of the lake, temperature variations resulting from the hydroelectric development were minor, so population responses due to temperature were primarily related to weather. However, other regions (e.g. the large northern basins) experienced diversion-related declines in water temperature as well as the weather effects. Abundance declined in all areas following the cold years of 1978 and 1979, but subsequent recovery in the latter regions was delayed or arrested because of a permanent diversion-related lowering of water temperature.

In this study, a combination of long-term monitoring, intensive field study and experimental hypothesis testing was required to identify population responses to natural factors (e.g. weather) and separate them from those due to anthropogenic effects.

TABLE OF CONTENTS

ABSTRACT i

TABLE OF CONTENTS. iV

LIST OF FIGURES. vii

LIST OF TABLES xii

ACKNOWLEDGEMENTS xiv

FOREWORD xv

CHAPTER I. INTRODUCTION. 1

CHAPTER II. REVIEW OF THE PERTINENT LITERATURE 6

1. Environmental Impact Assessment and Monitoring in Aquatic Systems. 7

2. The Churchill-Nelson Hydroelectric Development and Southern Indian Lake 11

3. *Hexagenia* (Ephemeroptera: Ephemeridae). 15

CHAPTER III. POPULATION DYNAMICS OF *HEXAGENIA LIMBATA* (SERVILLE) AND *H. RIGIDA* MCDUNNOUGH (EPHEMEROPTERA: EPHEMERIDAE) IN SOUTHERN INDIAN LAKE, MANITOBA, CANADA: THE INFLUENCE OF TEMPERATURE. 19

ABSTRACT 20

INTRODUCTION 22

STUDY SITES. 23

METHODS. 27

Nymphal sampling 27

Life history analysis. 27

Mortality. 28

CHAPTER III. METHODS (CON'T)

Adult collections 30

Fecundity 31

Temperature and degree day analysis 32

RESULTS 34

Temperature 34

Life History. 34

Mortality 41

Size and abundance. 41

Adult emergence 44

Usefulness of a degree day (dd) model to predict Hexagenia development 47

Fecundity 47

DISCUSSION. 50

I. LIFE HISTORY. 50

Life cycles 50

Degree day requirements 53

Body size 55

Fecundity 58

Mortality 58

II. TEMPERATURE EFFECTS ON ABUNDANCE OF *HEXAGENIA* IN SIL . . . 61

CHAPTER IV. EGG HATCHING IN *HEXAGENIA LIMBATA* (SERVILLE) (EPHEMEROPTERA: EPHEMERIDAE) FROM SOUTHERN INDIAN LAKE MANITOBA: TEMPERATURE EFFECTS AND DIAPAUSE. 64

ABSTRACT. 65

INTRODUCTION. 66

CHAPTER IV (CON'T)

MATERIALS AND METHODS 67

Site description and collection of adults 67

Artificial insemination technique 69

Storage procedure 70

Treatments. 70

Diapause trials 72

RESULTS 73

Hatching success. 73

Development time. 75

Egg diapause. 77

DISCUSSION. 79

CHAPTER V. EFFECTS OF TEMPERATURE, FOOD QUANTITY, AND NYMPHAL REARING DENSITY ON LIFE-HISTORY TRAITS OF *HEXAGENIA* (EPHEMEROPTERA: EPHEMERIDAE) FROM SOUTHERN INDIAN LAKE, MANITOBA, CANADA. 88

ABSTRACT. 89

INTRODUCTION. 90

MATERIALS AND METHODS 92

Study animals 92

Experimental trials 92

RESULTS 97

Growth rates. 97

Mortality 104

Development 104

Adult size and fecundity. 106

DISCUSSION. 107

CHAPTER VI. LONG-TERM ABUNDANCE PATTERNS OF *HEXAGENIA* IN SOUTHERN INDIAN LAKE: THE EFFECTS OF WEATHER AND HYDRO-ELECTRIC DEVELOPMENT. 113

ABSTRACT. 114

INTRODUCTION. 115

MATERIALS AND METHODS 116

Sampling. 116

Calculation of atmospheric degree days. 118

Correlations between air temperature and Hexagenia abundance - whole lake. 119

Correlations between abundance and 3-yr mean temperature - regions 121

RESULTS 121

DISCUSSION. 129

CHAPTER VII. OVERALL SUMMARY. 134

LITERATURE CITED. 141

APPENDIX A: SEPARATION OF COHORTS FOR *HEXAGENIA LIMBATA* AND *H. RIGIDA* FOR EACH OF THE STUDY REGIONS ON EACH SAMPLING DAY 160

APPENDIX B: MORTALITY CALCULATIONS AND SURVIVORSHIP CURVES. . . . 173

APPENDIX C: RELATIONSHIP BETWEEN SUMMER TEMPERATURES AND WINDY WEATHER 183

LIST OF FIGURES

FIGURE

I-1. Natural and diversion flows of the Churchill River in northern Manitoba (latitude in °N, longitude in °W). 3

II-1. Drainage basins of the Churchill and Nelson Rivers in western North America (LWCNR 1975) 12

II-2. Mature male *Hexagenia limbata* nymph from Southern Indian Lake. 16

III-1. Sampling sites on Southern Indian Lake (dots), and location of Fisheries and Oceans (DFO) field camp (square). Arrows refer to major inflow and outflows 24

III-2. Frequency distributions for body length, head width, and wing-pad length (mm) for *Hexagenia rigida* in Opachuanau, Southern Indian Lake, Manitoba (1986). Cohort separation: different stippling patterns represent different cohorts . . 37

III-3. Summer bottom water temperatures (°C) in the four study areas in Southern Indian Lake, 1986-1988 35

III-4. Length-frequency distributions for *Hexagenia limbata* with cohorts superimposed. Lines bisect the midpoints of each cohort as a guide for following cohorts through time (different stippling patterns represent different cohorts). Numbers at the top of each distribution refer to the total numbers collected. A) Opachuanau B) Wupaw Bay C) South Bay East D) South Bay West. 39

III-5. Length-frequency distributions for *Hexagenia rigida* with cohorts superimposed. Lines bisect the midpoints of each cohort as a guide for following cohorts through time (different stippling patterns represent different cohorts). Numbers at the top of each distribution refer to the total numbers collected. A) Opachuanau B) Wupaw Bay C) South Bay East D) South Bay West 40

III-6. Periods of 90% emergence for *Hexagenia* in the four study areas and for Missi Bay, a small bay near the natural outlet of the lake, 1986-1988. Numbers beside each bar refer to total accumulated water dd>10°C for each summer. 46

III-7. Relationship between female subimago body length (both species combined) and fecundity (no. eggs/female) E=no. of eggs BL=body length 49

FIGURE

III-8. Relationship between exuvial body length for *Hexagenia* from Southern Indian Lake. N=nymphal (exuvial) body length S=subimago body length ▲ = ♂ ● = ♀ 51

III-9. Summary of 3-yr *Hexagenia* life cycle and the factors influencing abundance in Southern Indian Lake. 59

IV-1. Southern Indian Lake, Manitoba, with locations of adult collections (solid dots) and major lake inflow and outlets (arrows) 68

IV-2. Egg hatching treatments and results for *Hexagenia limbata*. Hatching success is expressed as mean % hatch (±S.E.), and development time is the number of days (d) required for hatch after warming to final treatment temperature 74

IV-3. Summary of *Hexagenia limbata* diapause trials. Eggs were allowed to hatch at 20°C, then the remaining unhatched eggs were cooled to mimic overwintering, and then rewarmed to 20°C. Mean % hatch (±S.E.) and time to hatch after warming (d) are given for each treatment 78

IV-4. Relationship between development rate (1/t) and incubation temperature for *Hexagenia limbata* eggs (data from Hunt 1953 (●); Flattum 1963 (o); Neave 1932 (x); and this study (▲)) 82

V-1. Instantaneous growth rates (%length/d) of mid-sized field-collected *Hexagenia* nymphs at a range of temperatures in the laboratory (Experiment 1). 101

V-2. Instantaneous growth rates (%length/d) of two size-classes of *Hexagenia limbata* nymphs reared in the laboratory at two food levels over a range of temperatures (Experiment 3). . . 102

V-3. Growth of *Hexagenia limbata* at three constant temperatures (8°, 15°, and 20°C), and two food levels (L=limiting, N=nonlimiting; see text for explanation). Arrows point to time of first emergence; dashed lines represent continuation of emergence period following last sampling date (only 60% of emergence was complete in the 15°C trial at the time experiments were terminated (450 d), but the entire emergence period is shown for the 20°C trials. 103

VI-1. Southern Indian Lake, with regions (numbers), whole-lake survey sampling stations (dots), and location of SIL camp and weather station. Arrows refer to major inflow and outlets. 117

FIGURE

VI-2. Annual air temperature accumulations >0°C (1969-1987), and whole-lake *Hexagenia* abundance (no.m^{-2}, 1972-1987) for Southern Indian Lake 120

VI-3. Relationship between *Hexagenia* whole-lake abundance (mean no.m^{-2}) and 3-yr accumulated air temperatures (>0°C) in Southern Indian Lake, 1972-1987. 125

VI-4. Comparison between observed *Hexagenia* densities and those predicted from the relationship in Fig. VI-3 126

VI-5. Relationships between *Hexagenia* abundance and 3-yr accumulated air temperatures for the 9 Regions in Southern Indian Lake, 1972-1987. Asterisks refer to level of statistical significance: *$p<.05$; **$p<.01$; ***$p<.001$ 127

VI-6. Comparison between observed *Hexagenia* densities and those predicted from the relationships in Fig. VI-5. Solid lines = predicted; dashed lines = observed 128

A-1. *Hexagenia limbata* nymph, with measures used for cohort separation 163

A-2. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia limbata* in Opachuanau, 1986-1988. See Table A-1 for explanation of stippling pattern. 165

A-3. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia limbata* in Wupaw Bay, 1986-1988. See Table A-1 for explanation of stippling pattern. 166

A-4. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia limbata* in South Bay East, 1986-1988. See Table A-1 for explanation of stippling pattern. 167

A-5. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia limbata* in South Bay West, 1986-1988. See Table A-1 for explanation of stippling pattern. 168

A-6. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia rigida* in Opachuanau, 1986-1988. See Table A-1 for explanation of stippling pattern. 169

A-7. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia rigida* in Wupaw Bay, 1986-1988. See Table A-1 for explanation of stippling pattern. 170

FIGURE

A-8. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia rigida* in South Bay East, 1986-1988. See Table A-1 for explanation of stippling pattern. 171

A-9. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for *Hexagenia rigida* in South Bay West, 1986-1988. See Table A-1 for explanation of stippling pattern. 172

B-1. Densities and survivorship curves for *Hexagenia* from Opachuanau, 1986-1988. Closed circles represent individuals from the first generation (e.g. cohort 1) and open circles are the second generation (e.g. cohort 1a). See Table A-1 for explanation of cohort numbers. 179

B-2. Densities and survivorship curves for *Hexagenia* from Wupaw Bay, 1986-1988. Closed circles represent individuals from the first generation and open circles are the second generation. See Table A-1 for explanation of cohort numbers. 180

B-3. Densities and survivorship curves for *Hexagenia* from South Bay East, 1986-1988. Closed circles represent individuals from the first generation and open circles are the second generation. See Table A-1 for explanation of cohort numbers. NS = no sample 181

B-4. Densities and survivorship curves for *Hexagenia* from South Bay West, 1986-1988. Closed circles represent individuals from the first generation and open circles are the second generation. See Table A-1 for explanation of cohort numbers. 182

C-1. Relationships between number of windy days (days with wind speed >10 km/hr for at least two consecutive hours) for July-August (A) and for July-September (B), with mean summer temperatures (July-September) for Southern Indian Lake weather station, 1978-1987 185

LIST OF TABLES

TABLE

III-1. Total accumulated degree days (dd) >10°C for the four study areas in 1986, 1987, and 1988. The predicted life cycle length is based on an assumed requirement of 2000 dd>10°C to complete development and the mean dd for each region 26

III-2. Total and summer mean *Hexagenia* abundances (all cohorts; $\bar{x}$±S.E) for the study regions in Southern Indian Lake, 1986-1988 36

III-3. Year-to-year mortality (%) of *Hexagenia* nymphs from the four study regions in Southern Indian Lake for 1986-1988 (See Appendix B for calculations). Mean summer abundance was calculated for each year class (e.g. 1-yr old, 2-yr old, etc.), and mortality was estimated as the % difference from one year to the next. Mortality between 3rd-1st yr, and between 4th-1st yr, refers to the total mortality between the last stage nymphs of one generation and the potential number of 1st stage nymphs of the new one. NS=no sample; * density too low to estimate mortality. 42

III-4. Mean nymphal exuvial length (mm) of emerging *Hexagenia limbata* and *H. rigida* collected from each study area in Southern Indian Lake during 1986, 1987, and 1988, and estimated mean fecundity (# eggs/female; $\bar{x}$±95% C.I.) for each region. 43

III-5. Accumulated degree days (dd) for *Hexagenia* development calculated assuming developmental thresholds of 8°C and 10°C. a) Total dd from egg to adult (1985 cohort). b) dd to emergence in the final year of development (all cohorts) 48

III-6. Maximum reported sizes for *H. limbata* nymphs from populations located from Texas to northern Manitoba, and requiring from 1-4 yr to develop 57

IV-1. Total number of days, number of days above 8°C, and degree days (dd) >8°C and >10°C required to initial hatch of *Hexagenia limbata* eggs exposed to different temperature treatments. Treatment numbers correspond to Fig. IV-2. The 12-d period of cooling to storage temperature and dd accumulated during cooling to storage temperature is included in counts for all except treatment 1. 76

V-1. Growth and mortality of mid-sized *Hexagenia limbata* and *H. rigida* nymphs reared in the laboratory at 10°, 15°, and 20°C ($\bar{x}$±S.D., n=16; Experiment 1). 94

TABLE

V-2. Growth and mortality of small *Hexagenia limbata* nymphs reared in the laboratory at two food levels and a range of temperatures and nymphal densities for 90 d ($\bar{x}$±SD); initial size for all treatments: 1.01 ± 0.02 mm; IGR = Instantaneous Growth Rate (Experiment 3) 98

V-3. Growth and mortality of large *Hexagenia limbata* nymphs reared in the laboratory at two food and nymphal density levels, and at a range of temperatures for 90 d ($\bar{x}$±SD), (Experiment 3) 99

V-4. ANOVA statistics used to test for temperature, food, and density effects on growth of *Hexagenia* reared in the laboratory. For each experiment, temperature was evaluated separately (regression analysis) and in conjunction with other factors (ANOVA). df=degrees of freedom; F=calculated F statistic for ANOVA; P=probability level; R^2=correlation coefficient. 100

V-5. Size, fecundity, and time from egg hatch to first emergence of *Hexagenia limbata* adults reared in the laboratory at 15° and 20°C ($\bar{x}$±SD); N=nonlimiting food level; L=limiting food level; see text for explanation (Experiment 2) 105

VI-1. Average dates of break-up and freeze-up, length of ice-free season, and mean summer temperatures (°C) for Southern Indian Lake, 1972-1987 122

VI-2. Results of correlation analyses between whole-lake *Hexagenia* abundance and air temperatures in Southern Indian Lake, 1972-1987; r^2 = correlation coefficient; p = probability level (see text for explanation) 124

A-1. Summary of probable and observed oviposition and emergence years for each cohort; stippling patterns given in Figs. A-2 to A-9, and corresponding to cohort numbers in Table B-2 and Figs. B-1 to B-4 164

B-1. Mean *Hexagenia* abundance (no.m^{-2}, $\bar{x}$±SE) at each sampling site on each sampling day, SIL, 1986-1988. 176

B-2. Mean cohort summer densities (no.m^{-2}, $\bar{x}$±SE). The first number in each cohort series is the density for the summer of 1986, followed by 1987, and 1988. b) second generation. . 177

B-3. Year-to-year mortality (%) of *Hexagenia* nymphs from the four study regions in SIL for 1986-1988 calculated from Table B-2 (see text for explanation, note that this table also appears in Chapter III as Table III-3 and is repeated here for ease of comparison. NS = no sample, * numbers too low to evaluate 178

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Finally, I'd like to acknowledge the constant support and encouragement of my husband, Patrick Crawford, who cheerfully endured my long absences while collecting field data, and my many moods during the collection, analysis, and writing up of the data.

FOREWORD

This thesis is presented in "paper-style" format. Four journal papers have, or are expected to result from the thesis project, although only three are presented in manuscript form in the thesis. One paper currently in press in AMBIO, is a summary of the project and includes parts of the introduction and the summary chapters from this thesis (Chapters I and VI). The other papers have been or will be submitted in essentially the form in which they appear in the thesis. Chapter VI will appear as a Canadian Fisheries and Marine Services Technical Report from the Freshwater Institute.

CHAPTER I

INTRODUCTION

INTRODUCTION

A basic problem in monitoring industrial developments is discriminating between natural ecosystem variability and anthropogenic effects. Although good examples of the possible confusion of these factors exist for marine habitats (Bowman 1978, Cullinane and Whelan 1983), few are available for freshwaters. Between 1972 and 1987, results from benthic surveys of Southern Indian Lake (SIL), northern Manitoba, provided an example of how the causes of dramatic changes in standing stocks of biota can be misinterpreted.

SIL, a large lake on the Churchill River, is part of a major hydroelectric development in northern Manitoba. Manitoba Hydro's long-term plan to develop the 10,000-MW hydroelectric potential of the nearby lower Nelson River called for diversion of ≈850 $m^3.sec^{-1}$ of water (≈75% of total flow) from the Churchill River into the Nelson catchment at SIL (Newbury *et al.* 1984). The Churchill flows into SIL from the southwest and, prior to diversion, exited from the northeast on its way to Hudson Bay (Fig. I-1). In 1976, the natural outlet of SIL was dammed and water levels in the lake rose 3 m. By fall 1977, the diversion was operating at full capacity through a newly excavated channel leading from the southeastern part of the lake into the Nelson catchment (Fig. I-1).

Standing stocks of the benthic macroinvertebrate community as a whole responded to impoundment by initially increasing, then decreasing to near pre-impoundment levels (Giberson *et al.* 1991). A post-impoundment "trophic upsurge", typical of new reservoirs, results from an initial input and then subsequent depletion of nutrients and organic matter originating from newly flooded land. However, an opposite pattern to the apparent trophic upsurge was observed for burrowing mayflies (*Hexagenia*): lakewide standing stocks increased slightly following impoundment (1977 survey), but declined after

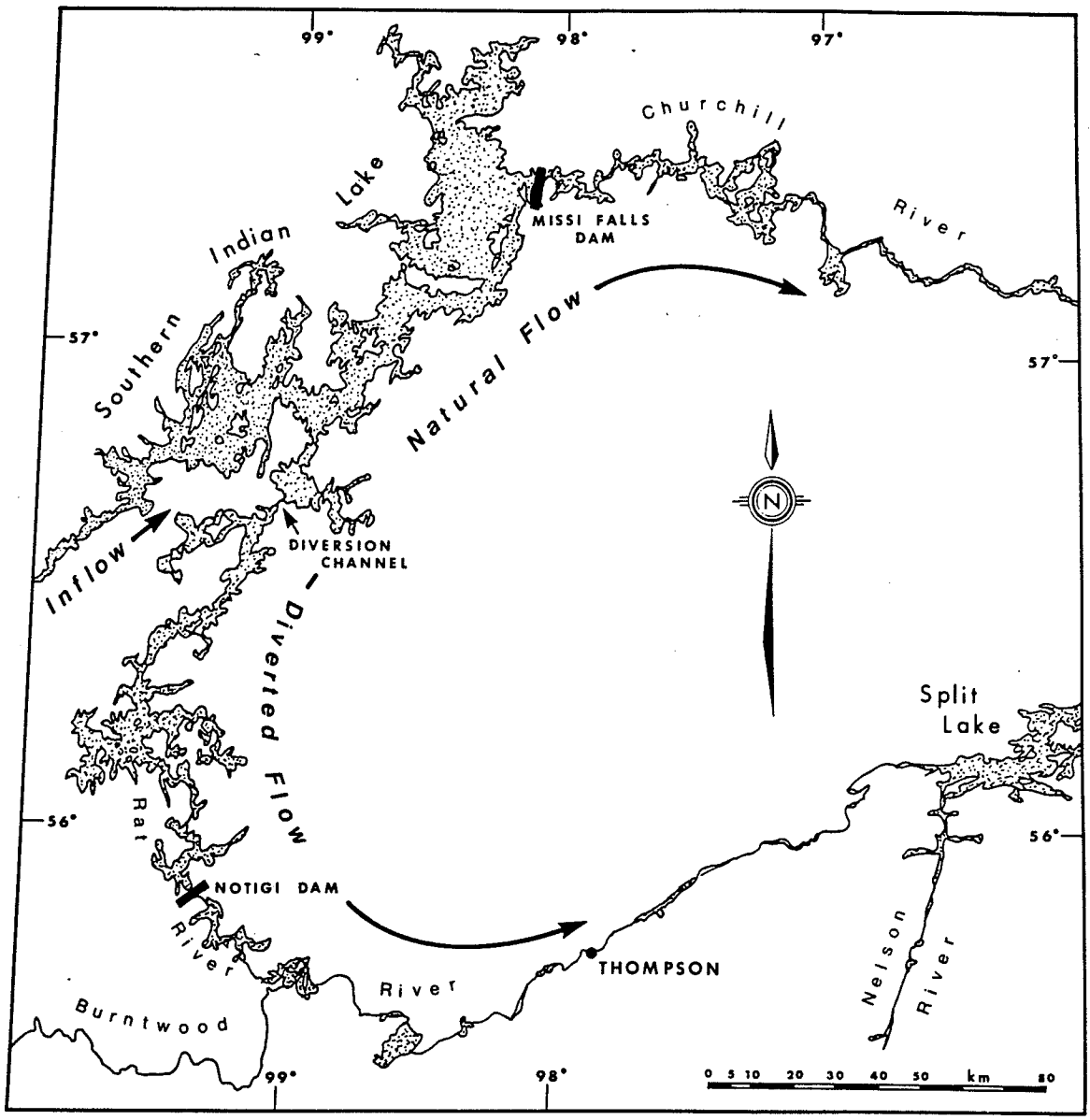

Fig. I-1. Natural and diversion flows of the Churchill River in northern Manitoba (latitude in °N, longitude in °W).

full diversion to ≈15% of the pre-development level (1981 survey; Giberson *et al.* 1991). Following the 1983 survey, the reduction in *Hexagenia* standing stocks was attributed to an inability by *Hexagenia* to maintain their burrows in the sediment because of severe shoreline erosion and altered substrate composition, and to a decrease in water temperature in the northern part of the lake because of river diversion (Rosenberg and Wiens 1985). However, sampling of the lake continued through 1987 and a partial recovery of the population was observed, despite the fact that impoundment and diversion still affected the lake.

It seemed likely that some other factor or factors besides those relating to the hydroelectric development were responsible for the observed decline in *Hexagenia* numbers. Because those factor(s) coincided with the development, interpretation of the monitoring data was confused, and the development was blamed. Factors that were considered as potentially important in controlling *Hexagenia* abundance were predation, food availability, and weather. Responses to predation were thought to have little effect on the observed pattern because the major predator of *Hexagenia* in SIL, lake whitefish (*Coregonus clupeaformis* DeKay), also declined following impoundment and diversion (Bodaly *et al.* 1984). If *Hexagenia* was responding to predation, numbers should have increased, rather than decreased, following the release of predation pressure. Similarly, if *Hexagenia* was responding primarily to food availability in the lake, abundance should have also increased after the development, due to increased nutrient and organic matter inputs from flooded shorelines. However, there was a strong correlation between air temperatures and lake-wide abundance of *Hexagenia* over the 15-yr monitoring period, suggesting that weather variables had an important influence on *Hexagenia* population dynamics (Giberson *et al.* 1991).

In 1986, an experimentally based autecological study was initiated to describe the life histories of *Hexagenia* spp. in SIL in relation to weather variables, in order to interpret the long-term survey data. The project consisted of two parts: 1) an intensive study of the population dynamics of *Hexagenia* in SIL under different weather conditions and thermal regimes and in the laboratory at different temperature, food and density levels, and 2) an application of this information to the interpretation of the survey data. Both *Hexagenia* species in the lake, *H. limbata* and *H. rigida*, were monitored in the lake and in preliminary experiments in the laboratory. However, an incubator failure during the study resulted in the deaths of laboratory cultures of *H. rigida*, so most of the laboratory experiments were conducted on *H. limbata*. The objective of the project was to determine the mechanisms of population control in SIL, in order to separate responses to natural factors from those relating to the development.

CHAPTER II.

REVIEW OF THE PERTINENT LITERATURE

1. ENVIRONMENTAL IMPACT ASSESSMENT AND MONITORING IN AQUATIC SYSTEMS

Aquatic ecosystems are valuable as sources of food, fresh water, faunal habitat, and recreation. Natural stresses that act on these systems include climate-related factors like temperature, wind-induced turbulence and mixing, and water availability. Anthropogenic stresses relate to industrial development or resource harvesting. "Stress" is defined as "any environmental factor that restricts growth and reproduction of an organism or population; any factor acting to disturb the equilibrium of a system" (Lincoln *et al.* 1982, p. 236). In practice, increasing public awareness of the deterioration of aquatic ecosystems has led to the perception that "stress" refers only to anthropogenic stress. This perception effectively prevents the separation of anthropogenic stresses from natural ones, since any changes (e.g. in population abundance or distribution) that are observed in a study of environmental impacts are assumed to stem from the industrial development being evaluated (Green 1984, Nichols 1985). If such were the case, detection of man-induced stresses would be a relatively simple matter, because all that would be required would be a description of spatial or temporal changes (Green 1984). However, mechanisms that influence population abundance are poorly understood in all but a few species, and population fluctuations relating to natural factors (e.g. weather, predation, competition) can dwarf or obscure potential anthropogenic ones (Nichols 1985). Our ability to detect man-induced ecosystem stresses must necessarily stem from the ability to characterize ecosystem responses to all types of stresses.

When evaluating ecosystem stresses, researchers are, in effect, looking at cause-and-effect relationships between the stress(es) and the ecosystem response. The most common way of doing this is to test a null hypothesis of "no change" against an implicit alternate hypothesis of "detectable change" in

the presence of the stress (assumed to be a change for the worse unless proved otherwise; Green 1984). The parameters of interest, e.g. abundance or biomass, are assumed to remain stable or vary predictably with time (e.g. seasonally; Nichols 1985).

However, both biotic and abiotic factors vary temporally and spatially in response to a variety of natural factors, many of which (e.g. climatic anomalies) cannot be predicted (Bakun 1986, Iker 1983; see Buchanan *et al.* 1978, Macan 1977, Northcote 1952, Oliver 1960, Schneider 1965, Stahl 1986, and Wright 1978 for examples). In many cases it is difficult, if not impossible, to exactly determine the mechanisms of population regulation in ecosystems, due to a complex interaction of events, all operating at different temporal and spatial scales and on different levels of organization (Hengevold 1987, Resh and Rosenberg 1989).

To illustrate this complexity, Carpenter *et al.* (1985) considered a hypothetical example in which a fluctuation in an abiotic parameter, such as abnormally low temperatures or water levels, might cause a recruitment failure of the dominant predator in a lake, a large piscivorous fish. This could lead to a temporary but significant decline in predation pressure on zooplanktivorous fish and, due to selective feeding on large zooplankton by zooplanktivorous fish, change the size structure of the zooplankton community. This in turn could result in pronounced differences in grazing and recycling rates, eventually affecting primary production (Carpenter *et al.* 1985, Scavia *et al.* 1986). In natural systems, sequences of cascading trophic interactions as described above will propagate from stochastic fluctuations, with lag effects occurring since generation times differ, and because trophic levels do not always remain constant (Carpenter *et al.* 1985). Concurrently, fluctuations in biotic and abiotic parameters may act directly on each level